

OBSERVATIONS OF FEEDING BEHAVIOUR IN TWO NEW ZEALAND MUD CRABS

(HELICE CRASSA AND MACROPHTHALMUS HIRTIPES)

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ABSTRACT

Feeding behaviour is described for the two burrowing mud crabs *Helice crassa* Dana 1851 and *Macrophthalmus hirtipes* (Jacquinot 1853) on mud flats near Christchurch, New Zealand. Both species feed mainly on organic matter extracted from surface mud but have developed different mechanisms for collecting food. *H. crassa* have spoon-tipped chelae which act as small scoops rather than scrapers, whereas the scraping chelae of *M. hirtipes* have setal sieves which allow organic material to be concentrated from unconsolidated mud before removal to the mouth.

INTRODUCTION

The brachyuran mud crabs *Helice crassa* Dana 1851 (Grapsidae) and *Macrophthalmus hirtipes* (Jacquinot 1853) (Ocypodidae) are endemic to New Zealand where they live in burrows on inlet or estuarine, tidal mud flats. Often they occur on the same mud flat, but *H. crassa* typically burrows in the more consolidated mud towards high tide limits whereas *M. hirtipes* is more common towards low tide limits in regions where mud is always waterlogged (Beer 1959). Their distributions often overlap.

Previously, Beer (1959) described agonistic behaviour and Nye (1974) outlined the burrowing behaviour of these crabs. The absence of any descriptions of the feeding behaviour of *H. crassa* and *M. hirtipes* and the idea that both species utilize the same food resources stimulated this comparative study.

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STUDY AREAS AND METHODS

Helice crassa was studied at two sites in the Avon-Heathcote Estuary, Christchurch ($43^{\circ}33'S$, $172^{\circ}44'E$); one in the Heathcote River and the other in front of the Mount Pleasant Yacht Club (Jones 1977). Some observations were made on *M. hirtipes* on mud flats near Linwood Avenue, Avon-Heathcote Estuary (Jones 1977), but the major study area for this species was located on marine mud flats at Governors Bay, Lyttelton Harbour ($43^{\circ}37'S$, $172^{\circ}39'E$). The latter mud flats are extensive with very little slope and remain waterlogged up to high tide limits. *M. hirtipes* occurred over most of these flats to the exclusion of *H. crassa*.

All observations of feeding behaviour were made through field-glasses or, in the case of *H. crassa*, by direct observation through slats in a launching ramp at Mount Pleasant Yacht Club, Avon-Heathcote Estuary. Feeding populations of both crabs were observed between 10.00 h and 16.00 h on dry, sunny days, and at all stages of the tide during March 1978.

RESULTS AND DISCUSSION

HELICE CRASSA

Beer (1959) found that *H. crassa* was most active, burrowing and feeding, when exposed at low tide. This observation was confirmed in this study although some crabs were also observed feeding while they were covered by water at high tide. Their behaviour at this time did not appear to differ markedly from those feeding at low tide but only a small proportion of the population emerged from their burrows. Some animals in the Heathcote River had burrows which were not covered by the high tide. These crabs fed normally at full tide whereas most crabs occurring further down the bank emerged only after their burrows were uncovered. As a general rule, emergence from burrows was associated with low tide and crabs began appearing on the mud surface in large numbers within 10 minutes of their burrows being uncovered.

In many areas sea lettuce, *Ulva lactuca*, was deposited on the mud surface as the tide receded. This covered and, in some instances, plugged the crab burrows. Emerging crabs forced their way through the algal plug and then cleared their burrow entrances either by grasping the alga with their chelae and dragging it away, or more commonly by pushing it away against folded chelae. Once the burrow entrance was clear, most crabs cleaned themselves by remaining almost motionless in the burrow entrance so that their branchial chambers had access to burrow water. Water was then pumped across and through their mouthparts. This procedure presumably cleaned the branchial cavity and mouthparts of adhering mud particles. The tips of the chelae also were combed through the mouthparts during this pumping period.

Crabs then emerged onto the mud surface and either began feeding on stranded *Ulva* or on fine particulate organic matter from the surface mud. Small strips of *Ulva* were torn from the main mass by opposing motion of the chelae and were inserted into the mouth by one of the chelae. Bleached, decomposing *Ulva* was usually selected as food. On a few occasions, other encrusting green algae were torn from the rocks with the chelae and ingested. Crabs feeding on mud walked slowly forwards away from their burrows with their chelae held vertically in front of them. Tips of the chelae were raised and lowered systematically to touch or break the mud surface in front of the advancing crabs. This appeared to be a formal searching behaviour since such probing often continued for approximately 70 millimetres before any mud was taken up by the chelae and deposited in the mouthparts. Following such probing, a crab might stop and take several small pinches of mud from a small area to the top of the mouth-frame with alternate movements of chelae or sometimes using only one chela. The hands (propodi) of *H. crassa* chelae are rather inflated and smooth (Fig. 1) and are not well adapted for scraping or spooning surface deposits as in the case of many ocypodids e.g. *Scopimera inflata* as described by Fielder (1970). Instead the tip of the fixed finger is excavated as a small spoon which can be covered by the curved tip of the moveable finger (Fig. 2). Since only very small quantities of substrate can be brought to the mouthparts by a single chela movement, it should be of advantage to the crab to detect richest organic deposits before beginning to feed. This possibly explains the continued probing movements made throughout a feeding period.

The small scoops of mud are manipulated by the mouthparts, useful material is taken into the gut and waste accumulates at the bottom of the mouth-frame which is wiped away periodically by a chela. This waste or pseudo-faeces often disappears into the surface mud very quickly if it is wet but remains intact, although as small ill-defined pellets, on drier deposits. Branchial water is used in food separation by the mouthparts and as *H. crassa* has no obvious mechanisms, e.g. tufts of ventral setae, to draw surface or interstitial water into its branchial cavities, crabs must return to their burrows periodically and replenish their branchial water from water retained in the burrows.

H. crassa seldom forages far from its burrow (200 mm approximately maximum). Usually an individual crab repeatedly emerges from its burrow with much the same orientation so that a feeding area around a hole develops.

MACROPHthalmus hirtipes

Beer (1959) stated that at Papanui Inlet near Dunedin *M. hirtipes* is active (feeding and burrowing) when covered by water during the rising or falling tide. In the light of our low tide observations, however, it seems unlikely

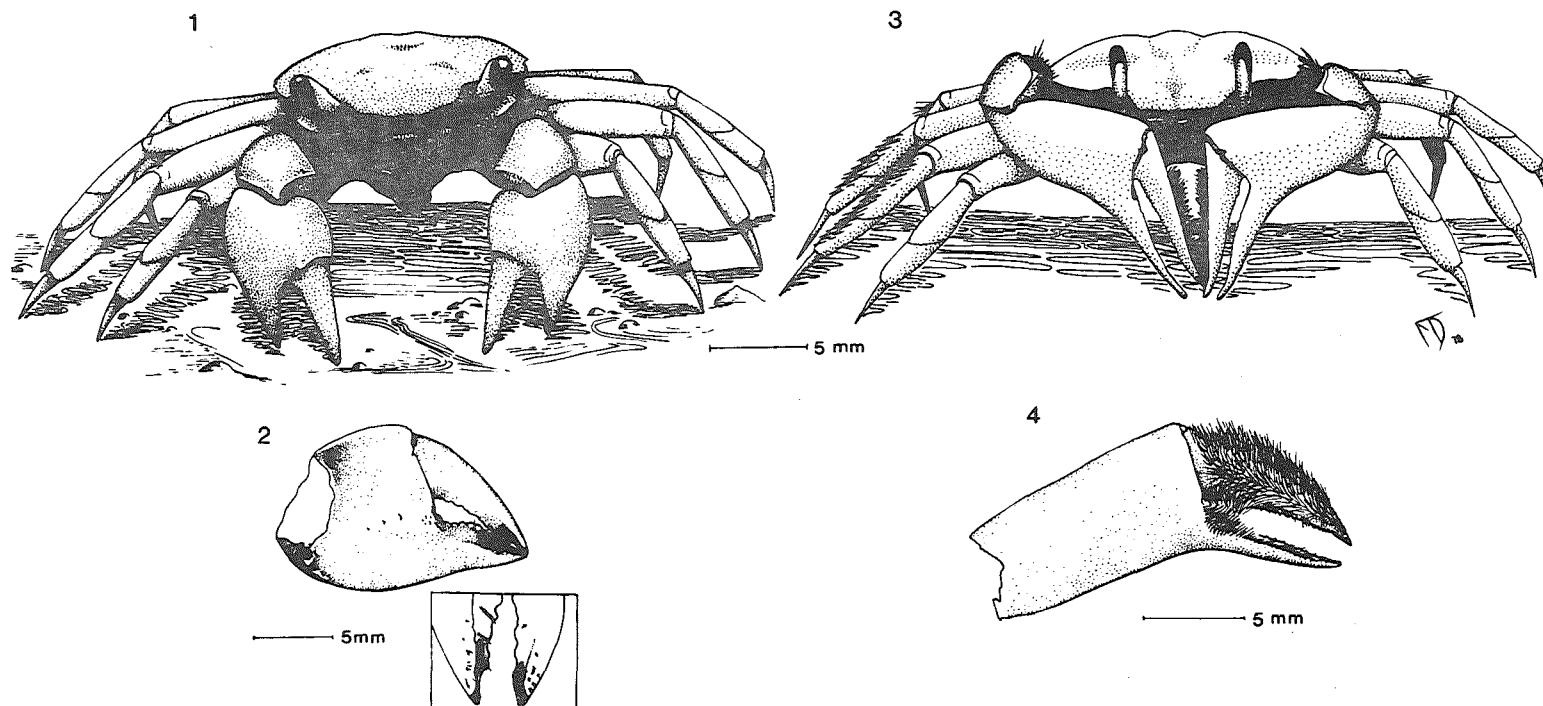


Fig. 1. Feeding pose of *Helice crassa*. Fig. 2. Detail of chela of *Helice crassa*. Fig. 3. Feeding pose of *Macrophthalmus hirtipes*. Fig. 4. Detail of inner face of chela of *Macrophthalmus hirtipes*.

that much feeding activity occurs at either Governors Bay or the Avon-Heathcote Estuary when the crabs are covered.

M. hirtipes moves sideways across the mud while feeding; it forages further from its burrow than *H. crassa* and, although most individuals return to their burrows intermittently during a feeding period, this is usually to protect their burrow against trespass rather than to replenish branchial water.

The entrances of most *M. hirtipes* burrows are located in shallow depressions which are filled with water even at low tide. Crabs began to emerge 10 to 15 minutes after the ebbing tide had passed their burrows. Often, emergence was preceded by a violent clearing of the burrows during which loose material was expelled from the entrance with sufficient force to produce a small geyser in the burrow pool. After emerging, each crab remained motionless for several minutes, either on more elevated mud or completely covered by burrow water except for the raised eyestalks. Similar cleaning activities as seen in *H. crassa* took place at this time. At Governors Bay, several different types of feeding area were available to the crabs. These included the mud at the bottom of the burrow pools, slushy mud which retained a substantial amount of surface water at the pool margins, and raised mud with a drier surface occurring between puddles. *M. hirtipes* utilizes all these areas using slightly different means of food collection.

In all forms of feeding, chelae were held more horizontal than vertical so that the downturned fixed fingers can act as scraper-scoops (Fig. 3). When feeding on drier surfaces, small scoops of mud were conveyed to the upper mouth-frame by chelae working alternately. Pseudofaeces presumably form as feeding proceeds but were never seen.

In soft slushy mud, the fingers of the chelae were held slightly open and then dragged laterally through the surface mud before being raised to the mouthparts. Usually both chelae scraped the surface simultaneously but food material was delivered to the mouthparts by alternate movements of chelae. The fingers of the chelae are fringed with setae (Fig. 4) which appeared to act as a sieve for concentrating food material from unconsolidated mud.

In shallow puddles, crabs raised themselves high off the substrate so that the hairy fringes of the walking legs, characteristic of this crab, trapped a film of capillary water and formed an open fronted receptacle beneath the crab's body. Water held loosely within this receptacle was stirred and mixed with bottom mud by the branchial currents and chelae. Chelae, again with slightly open fingers, were then used as scoops to drag the mixed slush up to the mouthparts.

A large proportion of the Avon-Heathcote flats inhabited by *M. hirtipes* consisted of compacted muddy sand, most of which retained a surface film of water at low tide. Here rather different food gathering mechanisms were utilized at low tide. The most commonly employed feeding method was to use the cupped chela fingers as scoops. The chelae were held nearly vertically and dug into the substrate

at least to the angle of the fingers. Quite large samples of the more consolidated substrate were then conveyed to the mouthparts by alternate movements of the chelae. Probing of the substrate by the chela tips was an associated part of this feeding behaviour as it was in *H. crassa*. Sometimes, usually after a prolonged period of probing, the vertically held chelae were dug into the substrate up to the meri and agitated to puddle it into a slurry. The chelae then returned to a more horizontal position and were used in the same way that crabs at Governors Bay worked very loose mud. The sieving setae of the chelae may also have been used at this time.

Another food source at both sites investigated was epiphytic algae growing on the shells of the mud snail *Amphibola crenata* (Martyn 1784) which was particularly abundant in the Avon-Heathcote Estuary. Fragments of epiphytes were torn from the shells by large crabs using their chelae and subsequently eaten.

It can be concluded that *M. hirtipes* is very adaptable in its feeding behaviour so that maximal use can be made of a variety of potential foods. In addition, feeding efficiency is increased by the presence of a mechanism for concentrating utilizable food before it is delivered to the mouthparts.

ACKNOWLEDGMENTS

We thank Mrs E.Y. Davie for the illustrations, the University of Canterbury for financial support, and Dr M.J. Winterbourn for improving the manuscript with his constructive criticisms.

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